The fossil record and phylogeography of the family Cerionidae (Gastropoda: Pulmonata), with the description of a new species from the Pleistocene of Florida

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ABSTRACT

Cerion petuchi, new species, the first record of the genus from the Pleistocene of Florida, is described from Loxahatchee, Florida, from deposits of the Loxahatchee Member of the Bermont Formation (Aftonian Pleistocene). This new species is more similar to *Cerion agassizii* from the Pleistocene of the Creat Bahamas Bank, and to the Recent *Cerion incanum saccharimeta*, from the Florida Keys, than to either of the species from the Late Oligocene—Early Miocene Ballast Point Silex Beds of Tampa, Florida. Data on the geographic distribution and geological age of all known cerionids is compiled and, together with models of the geologic and tectonic history of the Caribbean region, used to construct a hypothesis of the origins, ages, and relationships among the various lineages within the family since the Upper Cretaceous. The early distribution of the family was governed primarily by overland dispersal and vicariance. It is suggested that the significant proliferation of diversity that began during the Pleistocene is due to the increased prevalence of stochastic dispersal of small propagules (either by rafting or hurricane-born) among the islands of the Cuban and Bahamian archipelagos. Sea level changes caused by Pleistocene glaciations amplified diversity by repeatedly and sequentially recombining / hybridizing and isolating neighboring populations. Amplification of diversity would have been greatest on the Creat Bahama Bank, as it had the highest number of islands that were isolated during interglacial periods and conjoined during glaciations.

Additional keywords: Cerion, diversity, zoogeography, vicariance, dispersal

INTRODUCTION

The family Cerionidae has long been known for its exceptional morphological diversity and the profusion of species level taxa in the Recent fauna (e.g., Maynard, 1889–96; Pilsbry, 1901–02; Clench, 1957; Woodruff, 1978). In contrast, the fossil record of the Cerionidae, which extends from the Upper Cretaceous (Roth and Hartman, 1998), is poorly known and represented by comparatively few taxa, most based on rare specimens. A notable exception is in the fauna of the Bahamas, where *Cerion* are locally common in Pleistocene and younger deposits (Hearty and Kaufman, 2009). The geographic and ecological ranges of the family have recently been expanded considerably by inclusion of the genera *Brasilennea* from the Paleocene of the Itaboraí Basin, Brazil (Salvador et al., 2011; Salvador and Simone, 2012), and *Mexistrophia*, from cool, coniferous forests in the highlands of central Mexico (Thompson, 2012).

Within Florida, Cerionidae is represented by two species (one with two subspecies) from the Late Oligocene–Early Miocene Ballast Point Silex Beds of Tampa, Florida, and by a single native Recent species (subdivided into four subspecies) that is confined to the Florida Keys. Thirteen non-native species from the Bahamas, Cuba, Puerto Rico, and Curaçao were intentionally introduced into the Florida Keys and Dry Tortugas between 1912 and 1924 by Paul Bartsch as part of a long-running and well-documented series of experiments (see Harasewych and Strauss, 2006: Table 1). An additional taxon, *Cerion tridentata costellata* Pilsbry, 1946, despite a type locality of Garden Key, Florida, is a hybrid of two of the introduced Cuban species (Harasewych et al., 2011).

One complete and one partial specimen of *Cerion* have recently been discovered in Loxahatchee, Florida, from fossil deposits of Pleistocene age (Bermont Formation). These specimens represent a previously undiscovered species that is described as new and compared to fossil and Recent congeners.

The diversity of the family Cerionidae is reviewed from geographic and temporal perspectives. These results are combined with paleogeographic reconstructions of the Caribbean region (Iturralde-Vinent, 2006) to produce a zoogeographic hypothesis for the dispersal of Cerionidae during the Late-Cretaceous and Cenozoic. A recently published molecular phylogeny of Cerionidae

Table 1. Diversity of species level taxa within the family Cerionidae throughout its geographic and geological range. Data derived from the Cerion website [http://invertebrates.si.edu/cerion/] (Harasewych, 2009).

	TOTAL	Recent	Pleistocene/ Holocene	Pliocene	Miocene	Oligocene	Eocene	Paleocene	Upper Cretaceous
Montana	1								1
Florida[1]	8	4	1			3			
Mexico	3	3							
Little Bahama Bank	11	11							
Great Bahama Bank[2]	263	219	45						
SE Bahama Islands (Isolated Seamounts)[2]	33	32	2						
Turks and Caicos[3]	11	11							
Cuba	153	152	1						
Cayman Islands	16	16							
Hispanola[4]	4	4							
Puerto Rico + Mona[4]	2	2							
Western Virgin Islands[4]	2	1	1						
Aruba, Bonaire, Curaçao[5]	9	9							
Brazil	3							3	
TOTAL	519	464	50			3		3	1

(1) These figures do not include the species introduced into Florida by Bartsch during the first half of the 20th Century (see Harasewych and Strauss, 2006: Table 1), nor does it include *Cerion tridentata costellata*, which, despite a type locality of Garden Key, Florida, is a hybrid of introduced Cuban species (see Harasewych et al., 2011).

(2) Some species were reported both as Recent and Pleistocene.

(3) Clench (1961) synonymized six taxa from Turks Island under *Cerion regina* Pilsbry and Vanatta, 1895.

(4) Gould and Paull (1977) synonymized all living *Cerion* taxa from Hispanola, Mona Island, and Puerto Rico and the Virgin Islands under *Cerion striatellum* Guerin-Meneville, 1829, but retained as separate the fossil *C. rude* (Pfeiffer, 1855) from St. Croix.

(5) The Cerion of Aruba, Bonaire, and Curaçao had been subdivided into four subspecies some with large and dwarf named forms (Baker, 1924). Gould (1984) showed that the four subspecies correspond to geographic subdivisions, while the forms are non-adaptive ecophenotypic variations.

(Harasewych et al., 2011) is used to evaluate portions of this hypothesis.

SYSTEMATICS

Cerion petuchi new species
(Figures 1–11)

Diagnosis: Shell large (to 36 mm), with evenly tapering, conical spire, thick, finely ribbed, with broadly ovate aperture, widely flaring, simply recurved outer lip. Inner lip with parietal region broader than columella, each with a single tooth at mid-length. Umbilicus imperforate.

Description: Shell (Figures 1–9) large (holotype 36.05 mm long, 13.87 mm in diameter), thick, roundly conical in profile, with each whorl slightly broader than the preceding whorl. Protoconch (Figure 10) initially smooth, increasing in diameter from 504 µm to 3.26 mm in 2.6 whorls, with sculpture of 36 weak, evenly spaced axial ribs as broad as the intervening spaces appearing on the final half whorl. Transition to teleoconch (Figure 10, **p/t**) marked by an abrupt increase in shell diameter and onset of coarser surface sculpture. Teleoconch of 9⅛ evenly rounded whorls. Suture tightly adpressed. Axial sculpture of multiple (~96 on first teleoconch whorl, ~74 on final whorl) low rounded prosocline ribs (~18° to coiling axis) that generally align with interspaces of prior whorl. Spiral sculpture absent. Aperture expands, deflect-

ing suture adapically ~⅛ whorl prior to formation of thickened and flared terminal lip. Aperture broadly ovate, with the parietal wall forming an angle of 112° with the shorter columella. Single parietal tooth (Figure 11, **par**) emerges from mid-point of parietal callus. A weaker, broader tooth (Figure 11, **col**) recessed along mid-length of columella. Umbilicus imperforate, obscured by expanded terminal lip.
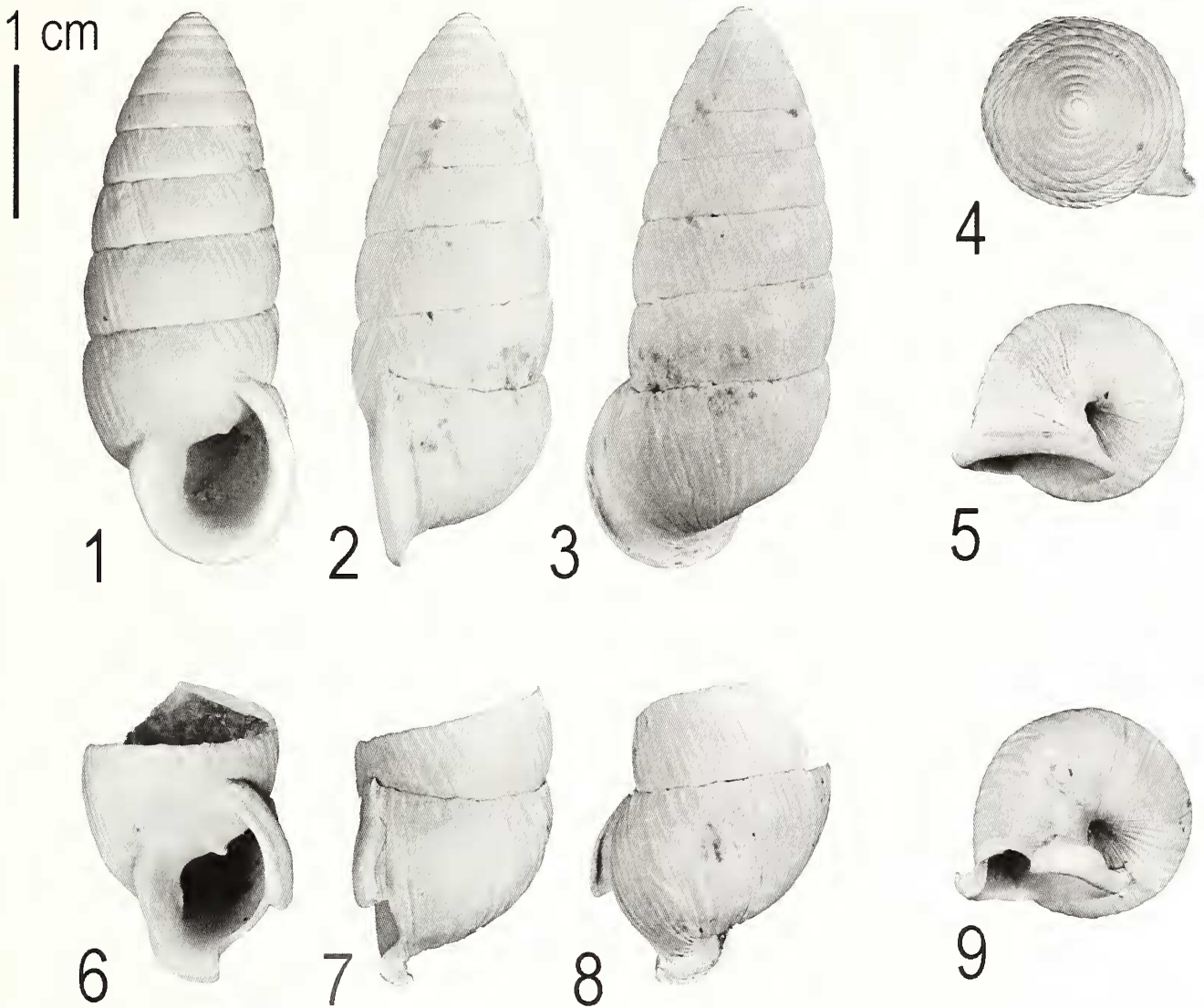
Type Locality: Palm Beach Aggregates, Inc. (old GKK) pit number 7, Loxahatchee, Palm Beach County, Florida [26°42.20′ N, 80°20.97′ W], at 15 m depth.

Stratigraphy: From the Holey Land Member of the Bermont Formation. Aftonian Pleistocene (~1.6 million years before present) (Petuch and Roberts, 2007: 147–162).

Type Material: Holotype, USNM 1191690; Paratype 1, USNM 1191691, both from the type locality.

Distribution: Known only from the type locality. This species was living in the Tomeu Paleoislands, along the northern end of Palm Beach Paleoarchipelago, Loxahatchee Subsea, Okeechoban Sea during the Aftonian Pleistocene (Petuch, 2003: fig. 31).

Etymology: This species honors Dr. Edward J. Petuch, who discovered it, in recognition of his many contributions to our understanding of the Recent and
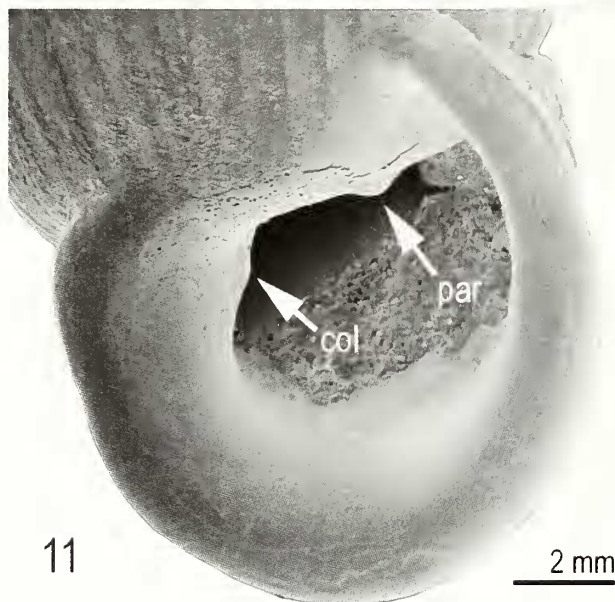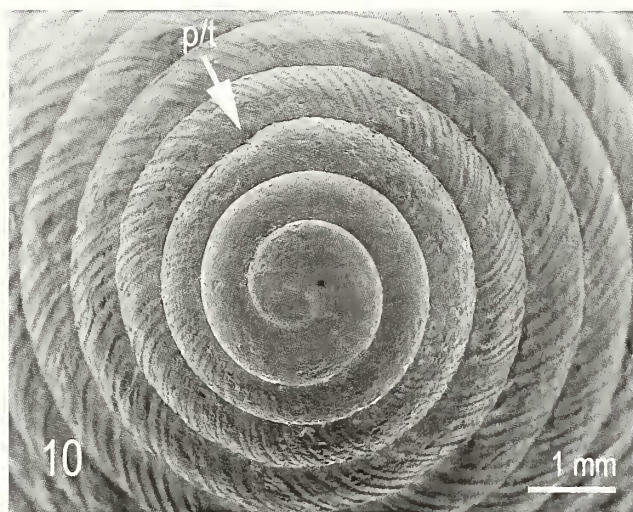
Figures 1–9. *Cerion petuchi* new species. **1.** Apertural, **2.** Lateral, **3.** Dorsal, **4.** Apical and **5.** Anterior views of the holotype (USNM 1191690). **6.** Apertural, **7.** Lateral, **8.** dorsal, and **9.** Anterior views of paratype fragment (USNM (X1191691). Palm Beach Aggregates, Inc. pit number 7, Loxahatchee, Palm Beach County, Florida. [26°42.20′ N, 80°20.97′ W] At 15 m depth. Holey Land Member of the Bermont Formation. Aftonian Pleistocene (~1.6 million years before present).

fossil molluscan faunas of Florida and the tropical western Atlantic.

Remarks: The large size, conical shell shape, presence of multiple, fine, axial ribs and a simple, flared lip serve to distinguish *Cerion petuchi* new species from all fossil cerionids reported from the Late Oligocene / early Miocene silex beds of Ballast Point, Florida. *Cerion (Microcerion) floridanum* Dall, 1915 had a much smaller shell with smoothly rounded whorls and a distinctive, extremely broad, concavely rounded outer lip. Both *Cerion (Eostrophia) anodonta* Dall, 1890 and *Cerion (Eostrophia) anodonta* var. *floridanum* Dall, 1915 had shells that are cylindrical in shape, with a smooth surface and smaller, rounder apertures. Pilsbry (1946: 161) reported a single fossil specimen that he identified as

Cerion incanum from Clewiston, Florida, from the younger Fort Thompson Formation (Pleistocene). This specimen, originally in the McGinty collection, was not illustrated and could not be located.

Of the Recent *Cerion* inhabiting the Florida Keys, *Cerion petuchi* new species most closely resembles *Cerion incanum saccharimeta* Pilsbry and Vanatta, 1899, which is also characterized by its large size and conical shell shape, but differs in having coarser and more irregularly spaced axial sculpture, a rounder aperture and a simpler, less flared outer lip. *Cerion petuchi* new species most closely resembles *Cerion agassizii* Dall, 1894, from the Pleistocene (ca. 120,000 years BP) dunes of New Providence Island (Bahamas), a species that is readily distinguished on the basis of having fewer, more irregularly spaced axial ribs, more pronounced parietal and

Figures 10–11. *Cerion petuchi* new species. **10.** Apical view of protoconch of holotype. **11.** Details of apertural dentition of holotype.

columellar teeth, and a "duplex" outer lip, which forms a concavely rounded, bow-like structure most pronounced along the anterior margin of the aperture. *Cerion picturata* (Maynard and Clapp *in* Maynard, 1921) from Pleistocene/Holocene deposits on Cabbage Key in the Berry Islands (Bahamas) is also similar. It lacks the "duplex" outer lip, but differing in having coarser, more axially aligned sculpture. A similar phenotype survives in the Recent fauna of Guana Key, Berry Islands as *Cerion arbusta* (Maynard and Clapp *in* Maynard, 1919).

GEOGRAPHIC AND TEMPORAL DIVERSITY OF THE CERIONIDAE

Data on geographic distribution and geologic age for the 600 species level taxa within the family Cerionidae were

compiled based primarily on information from the *Cerion* website (Harasewych, 2009). Taxa were assigned to islands or island groups based on their type localities. Objective synonyms and *nomina nuda* were excluded, as were taxa with unknown [e.g., *Cerion cumingiana* (Pfeiffer, 1852)] or clearly erroneous type localities [e.g., *Cerion antonii* (Küster, 1847) from British Guiana], but subjective synonyms were generally counted as separate taxa. Results are shown in Table 1.

Several authors have noted the multitude of taxonomic names applied to the abundant phenotypes within the Cerionidae and speculated that the actual number of valid species may be on the order of 1–20% of the number of names now extant (e.g., Clench, 1957; Woodruff, 1978). Although the numbers of taxa appearing in Table 1 will inevitably be revised downward based on detailed systematic studies, certain patterns are striking and will likely persevere. Most conspicuous is the observation that by far the greatest diversity of Cerionidae occurs on the Great Bahama Bank (47.2%, of all named Recent species level taxa), while the fauna of Cuba comprises 32.8% of all Recent species level diversity. Both these areas have alternated between being large, contiguous land masses and archipelagos during the glacial and interglacial sea-level fluctuations of the Pleistocene and Holocene. Iturralde-Vinent (2006:figs.7,8,10,11) has shown that Cuba consisted of a series of isolated islands from the Oligocene to the Late Pleistocene, with the present shape of the island attained 8,000–6,000 years ago.

By contrast, the combined fauna of the southeastern Bahamian Islands and the Turks and Caicos Islands, which would have remained isolated during the lowest sea levels, comprises only 9.3% of total Recent cerionid diversity. None of the remaining regions populated by cerionids contribute more than 3.5% of the Recent diversity.

This pattern is even more pronounced during the Pleistocene / Holocene, when the Great Bahama Bank accounted for 90.0% of the 50 described species level taxa. The isolated southeastern Bahamian Islands collectively accounted for 4.0% of the named fauna, with only single species (2.0% of the fauna) reported from Cuba, Florida and the western Virgin Islands. Prior to the Pleistocene, the fossil record is exceedingly sparse, with only three taxa reported from the Oligocene, three from the Paleocene, and one from the Cretaceous.

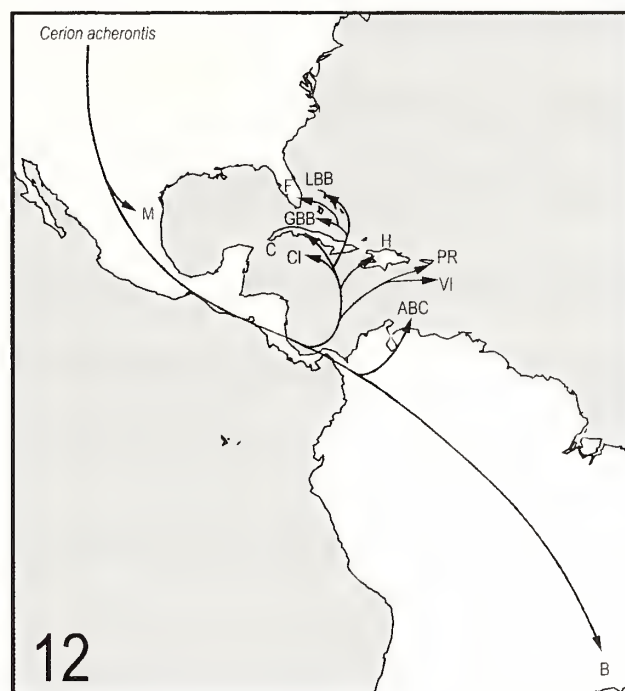## A ZOOGEOGRAPHIC HYPOTHESIS FOR CERIONIDAE

The early fossil record of the Cerionidae consists of few taxa represented by rare specimens that nevertheless provide insights into the zoogeographic history of the family. The earliest record for the family (*Cerion acherontis* Roth and Hartmann, 1998) is based on a single, damaged specimen from the Late Cretaceous of Montana. The genus *Brasilennea*, represented by three species from the Paleocene of Itaboraí Basin, Brazil, (Salvador et al., 2011; Salvador and Simone, 2012) has

recently been transferred from the family Streptaxidae to the Cerionidae. Western Laurasia (North America) and western Gondwana (South America) were separated by a marine waterway during the Jurassic (Callovian), with land bridges developing during the Late Cretaceous (Campanian / Maastrichtian) (75–65 Ma) via a proto-Antillean island arc, and again during the Plio-Pleistocene (2.5 Ma) via the Panama land bridge (Iturralde-Vincent, 2006). Parodiz (1969: 189, Map 7) noted that many of the families of South American non-marine mollusks are of Nearctic origin, having migrated to South America at the close of the Cretaceous. Given the presence of cerionids in South America during the Paleocene, it is probable that members of this family were part of this Late Cretaceous migration.

The recent description of the genus *Mexistrophia* from cool, coniferous forests in the highlands of central Mexico (Thompson, 2012), suggests that this genus was an early offshoot that diverged during the Late Cretaceous, prior to the adaptations to near shore, halophilic habitats of most living cerionids.

Uit de Weerd (2008: 323, fig. 8) explored a vicariance model in which the proto-Antillean island arc may have carried North American lineages, including Cerionidae and Urocoptidae, northeastward during the early Tertiary until it collided with the Bahamas platform during the Middle Eocene (Pindell, 1994). However, Iturralde-Vincent (2006) noted that it was not until the Middle Eocene that permanent lands, required for the development of a terrestrial fauna, were present within the Caribbean realm. An alternative hypothesis, that a mid-Cenozoic GAARlandia (GAAR = Greater Antilles + Aves Ridge) land bridge provided the means for colonization of the Greater Antilles from northwestern South America (see Iturralde-Vincent, 2006: fig. 6) during a 1–2 Myr interval at the Eocene-Oligocene boundary has been proposed (Iturralde-Vincent and MacPhee, 1999, see Ali, 2012 for a review). Iturralde-Vincent (2006: fig. 13) provided a detailed account of the patterns and chronology of interconnections among the various land masses within the Caribbean. This model is applied to produce a zoogeographic hypothesis for the distribution of Cerionidae since the Cretaceous (Figure 12), and is concordant with the absence of cerionids in Jamaica and the Lesser Antilles.

As there was never a land connection between Cuba and the Bahamas, the Great Bahamas Bank must have been populated initially by propagules from Cuba or the Cuban archipelago dispersed by hurricanes, with the Little Bahama Bank colonized by propagules from the Great Bahama Bank. The role of hurricanes in dispersing propagules of *Cerion* among neighboring islands has been accepted as stochastic events with a major influence on biogeographic patterns of cerionids (e.g., Pilsbry, 1907; Mayr and Rosen, 1956; Clench, 1957). Like Cuba, the islands of the Little and Great Bahama Banks were sequentially conjoined and separated by changes in sea level resulting in multiple instances of secondary contact between populations isolated during interglacial high

Figure 12. Hypothesized zoogeographic history of the family Cerionidae based on the age and distribution of fossil and Recent Taxa (Table 1) and paleogeographic reconstructions of the Caribbean region from the Cretaceous to Recent (Iturralde-Vincent, 2006). **ABC,** Aruba, Bonaire and Curaçao; **B,** *Brasilennea*; **C,** Cuba; **CI,** Cayman Islands; **F,** Florida; **GBB,** Great Bahama Bank; **H,** Hispaniola; **LBB,** Little Bahama Bank; **M,** *Mexistrophia*; **PR,** Puerto Rico; **VI,** western Virgin Islands

stands. Thus, populations that were isolated on small, individual islands during interglacial periods were able to expand their ranges and interbreed during glacial periods.

The islands of the Turks and Caicos and many of the southeastern Bahamian islands never had direct connection with the Bahama Banks or Cuba, and remained isolated by deep channels even during glacial sea level minima. The cerionid faunas of these islands are thus the summation of hurricane-born propagules reaching their shores from Cuba, Hispaniola, and the Bahamian Banks and islands.

The Cayman Islands were joined to southeastern Cuba by shallow banks during the Pliocene and are likely to have been colonized by cerionids from this region.

Early authors (e.g., Binney, 1851; Pilsbry, 1902, 1907, 1946; Dall, 1905) considered the living *Cerion* of the Florida Keys to be derived from populations of northern Cuba. However, a molecular phylogeny based on partial sequences of the cytochrome c oxidase I gene (Harasewych et al. 2011:fig. 16) shows them to be most closely related to samples from Andros Island on the Great Bahama Bank. The occurrence of *Cerion petuchi* new species in the Pleistocene of southeastern Florida is consistent with a Bahamian origin for the cerionid fauna of the Florida Keys. However, the origin and

relationships of the upper Oligocene–lower Miocene
cerionids of the central west coast of Florida are enig-
matic. There was never a direct connection between
GAARlandia and Florida, although this large peninsula
altered current patterns that might have facilitated
rafting of a propagule from the northern portions of
GAARlandia or one of its subsequent archipelagos to
the west coast of Florida (Iturralde-Vinent, 2006: fig. 12).
Alternatively, a separate offshoot of the Late Cretaceous
Cerion acherontis may have extended eastward along
the northern shores of the Gulf of Mexico, reaching
the coast of central western Florida by the late Oligo-
cene. These are, at best, speculative scenarios for the
origin of a cerionid fauna that does not appear to be
ancestral to the Pleistocene or Recent *Cerion* of south-
eastern Florida.

The zoogeographic hypothesis depicted in Figure 12
was converted to a phylogenetic tree (Figure 13), with
dates attributed to several nodes based on Iturralde-
Vinent (2006: figs. 10, 13). Dashed lines represent faunas
for which molecular data is lacking. The solid lines rep-
resent branches that are supported by a molecular phy-
logeny of Cerionidae based on amino acid sequences of
a portion of the mitochondrial COI gene (Harasewych
et al., 2011: fig. 17).

The early history of the Cerionidae was determined
by overland dispersal and vicariance caused by tectonic
events. *Mexistrophia* was isolated from the South American
cerionids since the Upper Cretaceous by the formation
of a seaway brought about by the displacement of the
proto-Antillean island arc by the eastward movement of
the Caribbean Tectonic Plate from the eastern Pacific.
Cerion sensu stricto, which inhabits the islands of Aruba,
Curaçao and Bonaire, was isolated from the remain-
ing Caribbean lineages of *Cerion* by the break-up of
GAARlandia and continued displacement of the Antil-
lean blocks and terranes northeastward by the advance-
ment of the Caribbean Tectonic Plate. The opening of
the Mona Passage during the lower Miocene separated
the terrestrial faunas of Cuba and Hispaniola from those
of Puerto Rico and the Virgin Islands. Hispaniola was
separated from eastern Cuba during the mid to late Mio-
cene, while the Virgin Islands and Puerto Rico were last
joined during the Pliocene (Iturralde-Vinent 2006: fig. 13).
With the exception of Cuba, the *Cerion* faunas of these
islands are not diverse.

The absence of a land connection between the islands
of the Bahamas (or the Turks and Caicos Islands) and
the Greater Antilles precluded overland colonization.
Rather, these islands must have initially been populated
by small propagules dispersed from the Greater Antilles
either by rafting or carried by hurricanes. Over time,
Cerion likely reached the more remote islands of the
Bahamas and Florida by a stepping stone pattern. It is
interesting to note that Bartsch's introductions of *Cerion*
into the Florida Keys generally consisted of large
numbers of individuals (n=500) and the resulting colo-
nies remained unchanged for multiple generations (see
Bartsch [1920] for a summary). However, experimental
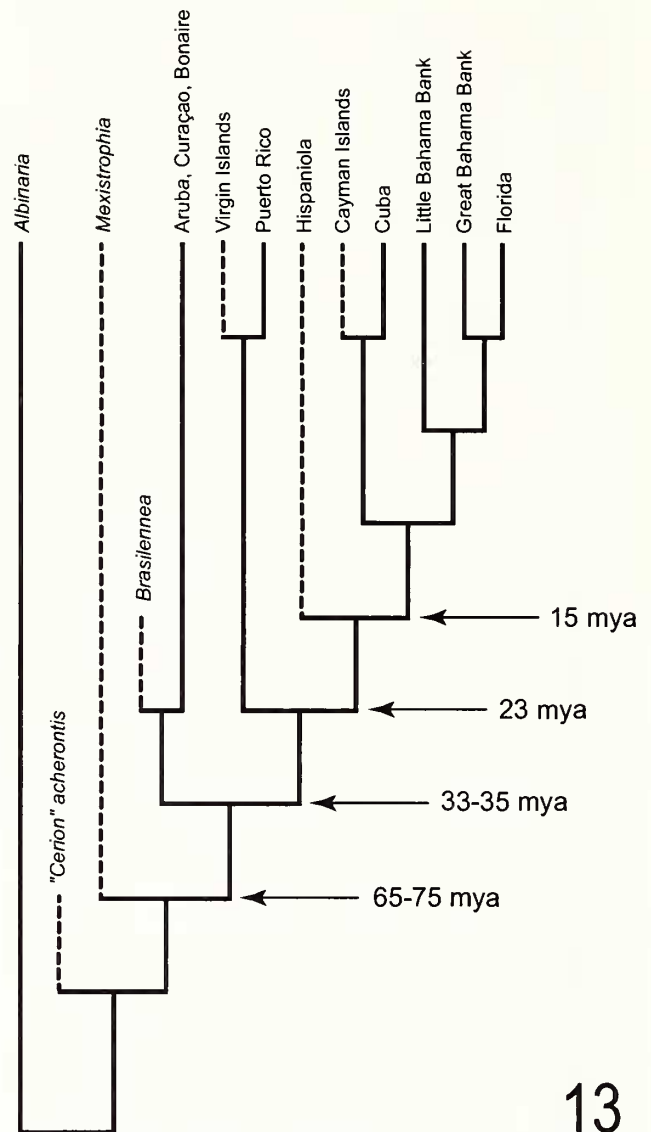
Figure 13. Phylogenetic relationships among living and fos-
sil cerionid faunas derived from phylogeographic hypothesis in
Figure 12. Solid lines represent portions of tree that are con-
cordant with a molecular phylogeny of Cerionidae based on
amino acid sequences of a portion of the mitochondrial COI
gene (Harasewych et al., 2011:fig. 17). Dashed lines represent
faunas for which molecular data is lacking. Dates attributed to
nodes are from Iturralde-Vinent (2006: figs. 10, 13).

introductions of *Anolis* lizards within the Bahamas using
much smaller propagules (5 or 10 individuals) resulted
in rapid differentiation over a 10–14 year period (Losos
et al. 1997).

Sea-level fluctuations caused by Pleistocene and Holo-
cene glacial / interglacial cycles altered the geography
and faunal diversity of individual islands to varying
degrees. During interglacial periods, terrestrial faunas
would be confined to isolated refugia on hill tops and
mountains that remained above the elevated sea-levels.
Drops in sea level during glacial periods would join the

islands of such archipelagos into larger platforms permitting previously isolated populations to expand their ranges and come into contact. Thus, such sea-level changes amplified diversity by repeatedly isolating and recombining / hybridizing neighboring populations of islands and banks defined during glacial periods.

The degree to which the diversity of a particular bank or island was amplified during a glacial cycle varied significantly, being a function of the number of islands that were united during glacial periods. The diversity of distinctive cerionid phenotypes (hybrids) on the Great Bahama Bank would have been greatly amplified by multiple cycles of glaciation due to the high number of islands that were isolated and conjoined. By contrast, the diversity of isolated islands such as San Salvador in the Bahamas, which remained isolated throughout the glacial cycles, would have changed little.

This ability of *Cerion* to hybridize, producing distinctive phenotypes and alozymes not present in either parent population, have contributed to the proliferation of taxonomic names, especially during the late 19th and early 20th centuries. Subsequent genetic and morphometric studies have shown that such novel phenotypes are often ephemeral, surviving on the order centuries (Woodruff and Gould, 1987) to millennia (Goodfriend and Gould, 1996). Further, all documented instances of hybridization have been between geographically and probably also phylogenetically proximal taxa [e.g., Hybrid on Bahia Honda Key, Florida = *Cerion incanum* (Florida) + *Cerion cassablancae* (Andros Island, Bahamas); Hybrid on Newfound Harbor Key, Florida= *Cerion incanum* (Florida) + *Cerion viaregis* (Andros Island, Bahamas); *Cerion tridentata costellata* Fort Jefferson, Garden Key, Dry Tortugas, Florida = hybrid of *Cerion tridentata* (Rincon de Guanabon, Cuba) + *Cerion sculptum* (Mariel, Cuba); Fossil hybrid on Great Inagua = *Cerion excelsior* (Great Inagua) + *Cerion rubicundum* (unspecified, but presumably a nearby island)]. None of Bartsch's experimental attempts to hybridize *Cerion* from Curaçao, Puerto Rico or Cuba with each other, or with *Cerion* from Florida or the Bahamas were successful.

ACKNOWLEDGMENTS

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